

Morphological variability of Upper Paleolithic and Mesolithic skulls from Sicily

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Summary - Scenarios for the dispersal of *Homo sapiens* in Southern Europe and in the Mediterranean basin have been uncertain, given the scarceness of osteological samples and the simplicity of the proposed archaeologically-based settlement hypotheses. According to available data, the first anatomically modern humans entered Sicily during the Late Pleistocene, coming from the Italian peninsula. A presumably small Late Epigravettian population colonised coastal sites. Later, North-Western archaeological horizons gave hospitality to a significant Mesolithic expansion. In order to verify a hypothesis of continuity in the peopling of the island, we analyzed Sicilian skulls from the Late Epigravettian site of San Teodoro, Eastern Sicily (AMS ¹⁴C dated at 14,500 BP) and from the Mesolithic period (¹⁴C dated from 9,500 to 8,500 BP) coming from various sites (Uzzo, Molara, Grotta d'Oriente) located on the North Western coast of the island. The aims were to test the biological variability through time within the island as well as to evaluate the relationships of Sicilian Pleistocene hunter-gatherers with Old World populations. We also evaluated the Sicilian Mesolithic uniformity especially between the Uzzo and Grotta d'Oriente sites, given their vicinity and accessibility during the Early Holocene. We applied 3D geometric morphometric methods to assess shape variation as well as geographic and diachronic morphological patterns. All analyzed specimens, plus a comparative sample from the Old World dated from the Upper Paleolithic to recent periods, were transformed in digital images and standard craniofacial landmarks were extracted from the 3D models. Our results underline a high variability among the Mesolithic specimens, as well as a large craniometric distance from the presumed founder Paleolithic settler representatives (San Teodoro specimens) that have closer morphological affinities with other European Upper Paleolithic specimens.

Keywords - Sicily, Upper Paleolithic/Mesolithic transition, Cranial shape, Geometric Morphometrics.

Introduction

Among the twenty administrative regions of Italy, only Sicily (the largest island in the Mediterranean Sea) has returned multiple samples of complete or near complete human adult crania dated to both the Upper Paleolithic and

Mesolithic archeological periods. More precisely, an Upper Paleolithic craniofacial sample comes from Late Epigravettian archeological horizons dated to the Late Glacial period of the Upper Pleistocene (ca. 17,000-11,700 cal. years BP), and several Mesolithic samples come from post-glacial, Early Holocene archeological

horizons (ca. 11,700-8,200 cal. years BP). Since craniofacial morphology, analyzed by geometric morphometric methods, is commonly used as a proxy for assessing genetic relationships among populations (e.g. Relethford & Harpending, 1994; Roseman, 2004; Harvati & Weaver, 2006; Manica *et al.*, 2007; Betti *et al.*, 2009; von Cramon Taubadel, 2009a,b, 2011a,b, 2014; von Cramon Taubadel & Weaver, 2009; Galland & Friess, 2016; Galland *et al.*, 2016; Reyes-Centeno *et al.*, 2017; Matsumura *et al.*, 2018, 2019; Relethford & Smith, 2018), the Sicilian record provides an opportunity to search for morphological affinities or differences between the two dated samples, in order to verify if significant morphological - and, consequently, biological - changes occurred on the island during the transition between the two periods.

If a Mesolithic transition took place - at least in Sicily - through a meaningful cultural/biological shift in local populations, it should be analyzed in connection with the climatic and environmental changes that occurred during the transition from the Pleistocene to the Holocene epochs, which could have caused the conditions for a new package of ecological pressures and resources available to humans. Indeed, the final part of the Pleistocene and the transition to the Holocene was characterized by increasing climate stability that created opportunities for hunter-gatherer groups to cyclically occupy areas in a move towards a mobile-forager/semi-sedentary ecology (Sineo *et al.*, 2015). By summarizing results of several studies carried out using both terrestrial and marine records, Incarbona *et al.* (2010) reported a review on the climate and environment in Sicily over the last 20,000 years. According to the authors, all the reconstructions of surface temperatures of the seas and of the air surrounding Sicily, point out severe climatic conditions during the last glacial period. Vegetation was characterized by a steppe or semi-steppe environment, but some surviving mesophilous and thermophilous species could have favored the rapid central Mediterranean re-colonization once climate amelioration happened (Sadori *et al.*, 2008; Incarbona *et al.*, 2010).

In the late Glacial, a period between 17,000 and 11,700 cal. years BP after the end of Last Glacial Maximum (LGM) associated with an overall climatic amelioration and the slow retreat of continental ice sheets in Europe, a “large” Sicily (due to the retraction of the sea water it was marked by an increase of about a third of the current emerged surfaces) was initially characterized by a cool and arid climate with a steppe-like ecology that lasted up to about 14,700 cal. years BP (Oldest Dryas stadial). The following transitional period toward the onset of the Holocene was punctuated by at least two abrupt suborbital climatic fluctuations, the Bølling-Allerød interstadial (a warm phase between 14,700 and 12,900 cal. years BP) and the Younger Dryas stadial (a cold phase between 12,900 and 11,700 cal. years BP), as recognized in the marine sediments (Incarbona *et al.*, 2010).

After the end of the Pleistocene, the Sicilian Mesolithic peoples who lived during the onset of the postglacial (Pre-Boreal and Boreal) in the Early Holocene (between 11,700 and 8,200 cal. years BP), experienced ecologically changing conditions characterized by increasing average temperatures and aridity of the climate (Zanchetta *et al.*, 2007; Sadori *et al.*, 2008; Incarbona *et al.*, 2010), with repercussions for faunal representation and human foraging that have been well documented in some key sites (Piperno, 1985).

Archeological evidence for Pleistocene human presence in Sicily is a highly debated topic (cf. e.g. Vaufray, 1928; Graziosi, 1950, 1968; Bianchini, 1969, 1971; Passarello, 1970; Biddittu & Piperno, 1972; Alimen, 1975; Segre *et al.*, 1982; Holloway, 1991; Bonfiglio & Piperno, 1996; Chilardi *et al.*, 1996; Tusa, 1997, 1999; Villa, 2001; Martini, 2003; Martini *et al.*, 2009; Lo Vetro & Martini, 2012; Sineo *et al.*, 2015). According to the present state of our knowledge, the earliest secure archeological record belongs to the late Upper Paleolithic period and is represented by stone artifacts related to the Late Epigravettian culture found sometimes in association with human skeletal remains. Well-excavated Mesolithic horizons lie in several sites, mainly caves, with conventional

^{14}C dates on archeological material ranging between $9,580 \pm 100$ and $7,040 \pm 55$ uncal. years BP, or between 9,250 and 6,480 cal. years BP (Lo Vetro & Martini, 2012; Sineo *et al.*, 2015).

At the present state of our knowledge, the skeletal record is reliably documented since the Late Glacial period of Upper Pleistocene (Sineo *et al.*, 2015); it represents a suitable evidence to study the early peopling of the island and to allow for some interpretative hypotheses concerning the history of its settlement. However, many remains are extremely fragmentary (see Supplementary Online Material Tab. S1 and the following text). The paucity of these finds does not allow much to be inferred concerning the physical aspect and the genetic relationships of the first inhabitants of Sicily, and highlights the importance of the most significant Late Pleistocene Sicilian site, the Grotta di San Teodoro (Acquedolci, Messina province). Several skeletal remains and archeological evidence of human frequentation were found in this cave site between 1937 and 1942, in association with faunal remains of the final Late Pleistocene Castello Faunal Complex and a Late Epigravettian lithic industry (Graziosi, 1947). The human osteological sample consists of seven adult individuals in various states of preservation, numbered as San Teodoro 1-7 (Mallegni, 2005c) (Supplementary Online Material Tab. S1). The geological age of the human skeletal remains was initially based on the typological features of the associated lithic industry attributed to Late (or Final) Epigravettian (between about 14,000 and 10,000 uncal. years B.P.) (Vigliardi, 1968; Bietti, 1990; Mussi, 2001). An AMS- ^{14}C dating essay has been performed directly on San Teodoro 1 specimen, obtaining a conventional radiocarbon age of $12,580 \pm 130$ years BP, with a calendar age (2s, 95.4%) of 13,283-12,177 cal. years BC or 15,232-14,126 cal. years BP, thus confirming a Late Glacial, Late Epigravettian age (Mannino *et al.*, 2011). A conservative estimate of 15,000-11,000 years BP remains the most probable date for San Teodoro individuals 2-4. A similar date is likely for individuals 6 and 7, although there is no precise information concerning their stratigraphic provenance. Individual 5, on

the contrary, was recovered from a higher level (Graziosi, 1947) and maybe could be a little more recent (D'Amore *et al.*, 2006). Six out of the seven individuals preserve craniofacial and/or mandibular parts, and five are sufficiently complete to have been included in previous general comparative studies of late Paleolithic and Mesolithic craniofacial morphometric evolution (e.g. Bianchi *et al.*, 1980; Henke, 1989). More recently, D'Amore *et al.* (2009) restudied the whole cranial sample by using linear craniometric traits and compared it to an array of both prehistoric and recent samples through different multivariate techniques. The resulting patterns of phenetic relationships illustrated the possible role played by San Teodoro people in the settlement of Sicily during the latest part of Pleistocene, favouring the hypothesis that they probably came from peninsular Italy by sea during the Late Pleistocene. A less probable hypothesis was that they descended from immigrants that arrived by land during a low sea level episode corresponding to the Last Glacial Maximum regression, about 18,000 years uncal. BP. Gene flow then caused these populations to become morphologically homogenous with the populations of peninsular Italy.

After the earliest settlement, a fairly large human skeletal record is available for the subsequent Early Holocene period. Precisely, this skeletal sample constitutes the richest one from the whole Italian country associated with Mesolithic archeological context. Sites such as Grotta della Molarola (province of Palermo), Grotta dell'Uzzo (province of Trapani) and Grotta d'Oriente (Favignana island in the Egadi archipelago) returned as many as seventeen individuals (listed in Supplementary Material Tab. S1). Direct ^{14}C dating (see Tab. 1) are available for Molarola 2 (8600 ± 100 years BP), Uzzo 5 ($9,270 \pm 100$ years BP) and Oriente B ($9,377 \pm 25$ years BP) individuals. Multidisciplinary research revealed many bio-anthropological aspects related to lifestyles, dietary habits, health conditions and subsistence strategies of these ancient peoples. Data mainly collected for the abundant Uzzo sample (Borgognini Tarli *et al.*, 1993) suggested

that adult individuals were a morphologically and metrically homogeneous population, characterized by low stature, low degree of sexual dimorphism and limb lateralization, but also by marked skeletal stoutness. Analysis of skeletal indicators of functional stress indicated a utilization of upper limbs in repetitive activities and intense involvement of lower limbs, load transportations for dorsal portion of vertebral column and overloading of the lumbar portion, and habitual squatting position. Dental wear/micro-wear and trace elements analysis suggested regular consumption of animal proteins, especially of marine origin (including whales and dolphins), but with relevance of vegetal components and a relatively sugar intake (Borgognini Tarli *et al.* 1993). Finally, good nutritional and health conditions were inferred, but with a high frequency of dental caries, anomalies and a strong wear.

Previous craniometric studies appeared to favour a continuity model. According to D'Amore *et al.* (2009, 2010), the whole San Teodoro cranial sample displays a morphometric pattern close to Western European groups of similar antiquity, in particular those from Central and Southern Italy, with their morphological affinities suggesting an origin from peninsular Italy during the Late Pleistocene. The whole Sicilian Mesolithic sample, on the other hand, appeared morphologically very close to an Italian Late Upper Paleolithic comparative group including San Teodoro. D'Amore *et al.* (2010) used linear craniometric traits for the whole Mesolithic adult cranial sample available from Sicily in order to assess the morphological affinities of the Oriente B skull in a comparative analysis with other late Paleolithic and Mesolithic samples from Italy and neighboring European areas. Multivariate techniques and significance tests were used in order to assess the role played by gene flow and drift to produce the resulting pattern of variation and relationships. Biodistance analyses showed that the Sicilian Mesolithic sample was morphologically very close to an Italian Late Upper Paleolithic comparative group; additionally, a general similarity among Western/Central European late

Paleolithic and Mesolithic groups was detected, thus suggesting a major role played by gene flow. R-matrix analysis confirmed that intensive gene flow among hunter-gatherer populations could account for the close resemblances among European late Paleolithic and Mesolithic groups. Instead, a chronologically decreasing trend of gene flow among populations, as detected by R-matrix analysis, for the transition from the late Paleolithic to the Mesolithic, and even more for the following main cultural transitions, could indicate the beginning of a certain level of regional characterization, with an increasing cultural and genetic isolation.

This research explores the key topic of diachronic biological variability within prehistoric Sicily (with a focus on the Upper Paleolithic-Mesolithic transition) as well as the relationship of Sicilian Pleistocene hunter-gatherers with other Old World populations and the degree of Sicilian Mesolithic population uniformity. The aim of the present study was to investigate if Early Holocene Mesolithic hunter-gatherers of Sicily could be the result of local evolution of Paleolithic individuals who migrated to the island during the Late Pleistocene or be the result of the overlapping of different and more recent migrations. In the first case Paleolithic gene flow from the Italian peninsula could have been the primer of human distribution on the island, producing a relatively uniform local characterization, as a result of similar ecological scenarios. Paleolithic hunter-gatherers could represent the effective genetic base of ancient Sicily while Mesolithic ones represent a cultural transition. In the second case, a relatively different gene flow (Mesolithic) could have contributed different people, their evolution inside the island having been shaped by the same ecological pressures.

Materials

Upper Paleolithic and Mesolithic craniofacial specimens from Sicily used in this study come from four sites (Fig. 1): Grotta di San Teodoro (Late Glacial, Late Epigravettian

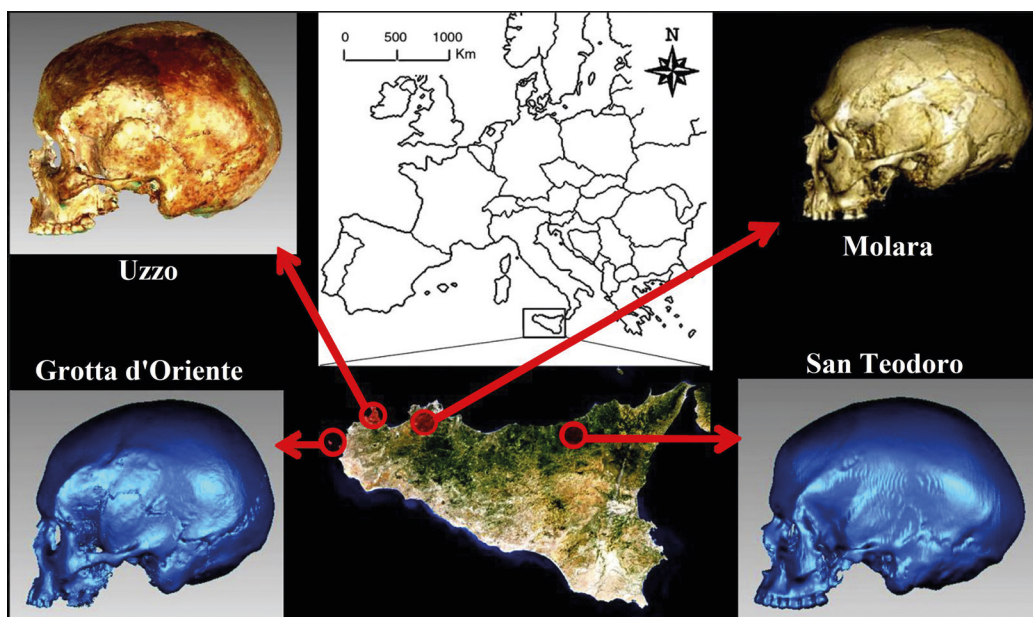


Fig. 1 - Map showing the area of the four Sicilian sites analysed and left lateral views of skulls from San Teodoro, Uzzo, Molara and Grotta d'Oriente. The colour version of this figure is available at the JASs website.

Upper Paleolithic), Grotta della Molara, Grotta d'Oriente and Grotta dell'Uzzo (Early Holocene, Mesolithic) (see Supplementary Online Material for archaeological and anthropological evaluations). An updated inventory shows that as many as nine Upper Paleolithic and twelve Mesolithic adult specimens, preserving the craniofacial portion and not consisting of isolated mandibular specimens only, are available for Sicily, whereas only a few Mesolithic specimens are available from all the other Italian administrative regions (see in Alciati *et al.*, 2005). However, we were able to include in our analysis only two Upper Paleolithic and seven Mesolithic specimens (Tab. 1), because of the need to select sufficiently complete skulls or at least skullcaps, and because of some samples being unavailable at institutions where some other complete specimens are actually housed.

Our comparative sample included 53 specimens from Upper Paleolithic and Mesolithic sites on the Italian peninsula and of other geographical regions of the Old World and Australia

(Tab. 1), and 210 specimens from 12 recent groups (Tab. 2). The absolute dates of Upper Paleolithic and Mesolithic specimens range from 5,480 to >153,00 years BP, although the oldest date for the Liujiang 1 cranium from China is presently debated, and it could actually be much more recent. Geographical provenances are from Italy, France, Germany, Czech Republic and Latvia in Europe; from Sudan in Northern Africa; from Israel in Western Asia; from China, Japan and Laos in Eastern Asia; and finally from Australia.

Methods

Data collection

All specimens were surface-scanned (Nextengine HD, www.nextengine.com; Breuckmann Smartscan stereo, www.breuckmann.com) or surface models were obtained from CT scans using a General Electric LightSpeed VCT 64 Slice CT multidetector scanner, with a

Tab. 1 - Details about the Upper Paleolithic and Mesolithic craniofacial sample listed by geographical region (Sicily, Italy, Europe, Middle East and Australasia). UP= Upper Paleolithic; Me= Mesolithic.

SITES AND SPECIMENS	ABBR.	LOCALITY	PERIOD	DATE YEARS BP ^A	REF.	N. SKULLS MISSING DATA (%) ^B	
San Teodoro 1, 2	ST	Sicily	UP	12,580±130	Mannino <i>et al.</i> (2011)	2	1.28
Uzzo 1, 2, 5, 6, 9	Uzz	Sicily	ME	9,270±100; 9,365±40; 8,856±37	Belluomini & Delitala (1983); Mannino <i>et al.</i> (2015)	5	18.8 (crania); 24.91 (neurocrania)
Molara 2	Mol	Sicily	ME	8,600±100	Gowlett <i>et al.</i> (1987)	1	2.56
Grotta d'Oriente B	OB	Sicily	ME	9,377±25	Mannino <i>et al.</i> (2012)	1	0
Arene Candide 2, 3, 4	AC	Italy	UP	between 9,925±50 and 10,735±55	Formicola (2005); Formicola <i>et al.</i> (2005)	3	5.98
Villabruna 1	Vil	Italy	UP	12,140±70	Alciati & Formicola (2005b)	1	0
Mondeval de Sora 1	MS	Italy	ME	7,425±55	Alciati & Formicola (2005a)	1	0
Abri Pataud 1	AP	France	UP	20,535	Brewster <i>et al.</i> (2014)	1	0
Bruniquel 24	Bru	France	UP	15,290±150	Brewster <i>et al.</i> (2014)	1	0
Chancelade 1	Cha	France	UP	Magdalenian, 11-12,000 as Oberkassel?	Brewster <i>et al.</i> (2014)	1	0
Cro-Magnon 1,2	CM	France	UP	27,680±270	Brewster <i>et al.</i> (2014)	2	10.25
Rond-du-Barry 1	RB	France	UP	17,100±150	Brewster <i>et al.</i> (2014)	1	0
Brno 3	Brn	Czech Republic	UP	Gravettian, 23,680±200 as Brno 2?	Brewster <i>et al.</i> (2014)	1	0
Mladec 1	Mla	Czech Republic	UP	31,190±400	Brewster <i>et al.</i> (2014)	1	0
Predmost 3	Pre	Czech Republic	UP	26,595	Brewster <i>et al.</i> (2014)	1	0
Oberkassel 1, 2	Obe	Germany	UP	11,570±110; 12,180±110	Brewster <i>et al.</i> (2014)	2	12.81
Zvejnieki 9, 37, 160, 199, 211, 241, 242, 252, 269	Zve	Latvia	ME	5,480-7,730	Zarina (2006); Brewster <i>et al.</i> (2014)	9	3.59
El Wad 10256, 10260	EW	Israel	UP	Natufian, 12,950-10,700	Bocquentin (2003); Cheronet <i>et al.</i> (2016)	2	2.56
Kebara	Keb	Israel	UP	Natufian, 12,470-11,150	Bocquentin (2003)	1	7.69
Ohalo 2	Oha	Israel	UP	19,000	Hershkovitz <i>et al.</i> (1995)	1	0
Wadi Halfa (6B36), 14, 20, 25, 32, 34, 35, 37	WH	Sudan	ME	10,000-13,000	Green & Armalagos (1972); Galland <i>et al.</i> (2016)	7	14.65
Liujiang 1	Liu	China	UP	>67,000; ~111,000- 139,000; >153,000	Mizoguchi (2011)	1	0
Minatogawa 1	Min	Japan	UP	18,250-16,600; 19,200	Mizoguchi (2011)	1	0
Tam Hang 3 (North), 2, 3, 4, 7, 10, 11, 13, 14, 22 (South)	TH	Laos	UP	15,700±800	Shackelford and Demeter (2012)	10	15.64
Upper Cave 101,103	UC	China	UP	10,000; 18,000; 24,000-34,000;	Mizoguchi (2011)	2	1.28
Wadjak 1	Wad	Indonesia	UP	37,400-28,500	Storm <i>et al.</i> (2013)	1	0
Keilor 1	Kei	Australia	ME	15,000; 12,900; 12,000	Mizoguchi (2011)	1	0
Total						61	

^AUncalibrated date; ^B Missing data estimated using Thin-Plate-Spline interpolation

Tab. 2 - Details about the recent comparative sample.

GROUP	ABBR.	LOCALITY	N SKULLS	MISSING DATA (%) ^A	MUSEUM ^B
Ainu	Ainu	North Japan	11	1.63	AMNH, MNHN, NHM
Andaman	And	Andaman Islands (India)	16	0.16	MNHN, NHM
Australian	Aus	Australia	25	0.82	MNHN, NHMV
Czech	Cz	Czech Republic	19	4.18	MNHN
Egyptian	Eg	Egypt	24	0.32	MNHN
French	Fr	France	13	0	MNHN
Tanzanian	Tz	Tanzania	13	0.39	Dw
Hungarian	Hg	Hungaria	11	0	NHNV
Mongolian	Mg	Mongolia	31	2.23	MNHN
Romanian	Rom	Romania	10	0	MNHN
South African	SA	South Africa	13	1.77	DCWU
Swedish	Sw	Sweden	24	2.35	MNHN
Total			210		

^A Missing data estimated using Thin-Plate-Spline interpolation

^B Abbreviations: AMNH = American Museum of Natural History (New York); MNHN = Muséum National d'Histoire Naturelle (Paris); NHM = Natural History Museum (London); NHMV = Natural History Museum of Vienna (Vienna); Dw = Duckworth Collection (Cambridge); DCWU = Dart Collection Witwatersrand University (Johannesburg).

gantry rotation time of 0.6 s, a slice thickness of 0.6 mm, and maximum intensity projection (MIP) utilized for integration. Data were saved as bit-map files in Digital Imaging and Commutations in Medicine (DICOM) format and processed and segmented using the open-source software 3D Slicer (Fedorov *et al.*, 2012). Shape data were then captured in the form of three-dimensional coordinates of osteometric points. Thirty-nine or twenty-two landmarks were respectively placed on each cranium or neurocranium for incomplete specimens by a single observer (MG) using the Landmark Editor software (Wiley, 2005). Anatomical descriptions of all landmarks are presented in Supplementary Material Table S2. Missing bilateral landmarks were estimated by mirroring-imaging and missing landmarks in the sagittal plane or bilateral landmarks missing on both sides were estimated by the tps (Gunz *et al.*, 2009) by deforming a sample average of the most similar configurations onto the deficient configuration (Schlager, 2012). All cranial and neurocranial landmark configurations have less than 20% of missing data (MD) with the exception of

Uzzo specimens (24.91% on average: 40.9% for U1A, 27.27% for U7, 33.33% for U1B, while 10.25% for U4A and 12.82% for U4B) (Tabs. 1, 2). In sum: in Upper Paleolithic (37 specimens) 21 specimens have MD, in Mesolithic (25 specimens) 19 specimens have MD, in Recent (210 specimens) 51 specimens have MD. Specimens missing the whole face were only included in the analyses based on neurocranial configurations. Repeatability was assessed through five non-consecutive landmarks collection on ten specimens. The standard deviation (mean 0.779 mm; Tab. S3) was below reported standard errors in craniometrics (Bräuer & Knußmann, 1988). The estimation of missing landmarks and all statistical analyses were performed using R (R Development Core Team, 2016).

Geometric morphometrics and multivariate analyses

Both sets of landmarks (complete skulls and neurocrania) were subjected to generalized Procrustes analysis (GPA, Gower, 1975; Rohlf, 2000) which allows the separation of geometric

shape from overall (isometric) size. Craniofacial landmark configurations were translated to a common centroid, scaled to unit centroid size, rotated by least squares fitting and then subjected to tangent space projection. This work focused only on the symmetric component of shape variation so all analyses are based on the averaged Procrustes coordinates of each landmark configuration and its mirror image (Klingenberg *et al.*, 2002). Patterns of shape variation and morphological affinities were explored with Principal Components Analyses (PCA). Shape differences were visualized along the PCA axes. Unrooted neighbor-joining trees (Saitou & Nei, 1987) were computed based on Procrustes distances to evaluate morphological affinities among specimens and groups without making assumptions about ancestry. The branch lengths of the tree also give indication about the degree of dissimilarity between groups. Neighbor-joining trees based on Procrustes distances were computed also on a subset of 17 European Upper Paleolithic and Mesolithic groups in order to make a comparison with only geographically proximal specimens to the Sicilian ones and to see what patterns may emerge without the effect of the vast geographic and temporal distances.

A partial Mantel test (Smouse *et al.*, 1986) was performed in order to explore the correlation between the Procrustes distance matrix and geographic distance matrix while controlling for the effect of the temporal distance matrix, as well as to explore the correlation between the Procrustes distance matrix and temporal distance matrix while controlling for the effect of the geographic distance matrix. A significant correlation between the Procrustes and geographic matrices is expected if gene flow was the main evolutionary factor producing the observed pattern of morphological relationships, and a significant correlation between the Procrustes and temporal matrices is expected if time had a major impact in producing the observed pattern of morphological relationships. Partial Mantel tests were performed with 9,999 permutations through the program *z*t Version 1.1, written and kindly made available on the web by E. Bonnet.

Geographic distances D between all the groups were calculated as great circles, distances in km according to the formula:

$$D = 2R \cdot \arctan \frac{\sqrt{\text{hav}(\Theta)}}{\sqrt{1 - \text{hav}(\Theta)}}$$

where

$$\text{hav}(\Theta) = \sin^2 \Theta \frac{\delta_1 \delta_2}{2} + \cos \delta_1 \cdot \cos \delta_2 \cdot \sin^2 \frac{\alpha_1 \alpha_2}{2}$$

with α_1 , δ_1 and α_2 , δ_2 being the average latitudinal and longitudinal coordinates, respectively, for groups 1 and 2, and R being the radius of the Earth (6371 km) (Ramachandran *et al.* 2005).

Temporal distances were obtained by calculating the difference in average dating between groups. In order to further investigate the relationships between Sicilian Upper Paleolithic and other samples, we compared the shape distance that separates the Sicilian Upper Paleolithic from the Sicilian Mesolithic to the distribution of pairwise distances within and between other subsamples. According to the hypothesis of a major change between Upper Paleolithic (San Teodoro material) and Mesolithic (Uzzo, Oriente B and Molará) in Sicily, the distance between these two groups is expected to be higher than the average within Mesolithic and within Upper Paleolithic distance.

Results

Cranial variation among Upper Paleolithic and Mesolithic specimens

Results based on a Principal Components Analysis on complete crania and neurocrania (Fig. 2) highlight the variability of Sicilian material and how these specimens do not form a distinct cluster among Upper Paleolithic and Mesolithic Old world fossils. Both datasets clearly separate Upper Paleolithic San Teodoro specimens from Molará, Uzzo and Oriente Mesolithic groups along the first axis. Shape changes show that San Teodoro specimens have a more prognathic and narrower face, especially ST1, a more projected glabella, a much narrower cranial vault, especially

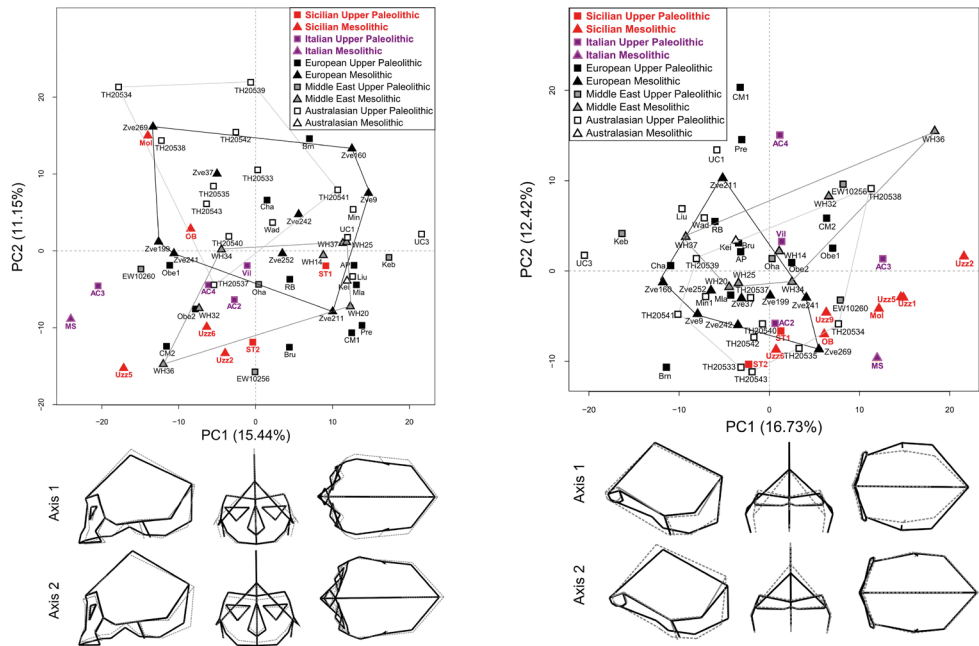


Fig. 2 - PCA based on Procrustes coordinates with shape changes among Upper Paleolithic and Mesolithic samples for crania (left) and neurocrania (right). Landmark configurations (lateral, frontal and superior views) represent the highest (bold) and the lowest (grey) scores. Polygons outline the distribution of the most numerous groups: Zvejniecki (black line), Wadi Halfa (dark grey line) and Tam Hang (light grey line). Abbreviations are in Tab. 1. The specimens numbers are indicated only in the case of several specimens by site. The colour version of this figure is available at the JASS website.

ST2, more evident in the neurocranial dataset, a less elongated occipital bone, shorter mastoid processes and a nasal aperture slightly narrower. While Mesolithic Sicilian specimens from the three sites are very close, especially when the neurocranium only is considered, craniofacial results illustrate a distinction on the second axis of variation between fossils from Molara and the three fossils from Uzzo. Uzzo 2 and Uzzo 6 are very close to each other and like Uzzo 5 have a longer cranial vault, a more projected glabella, a more elongated occipital bone, a lower face and vault, lower and wider orbital apertures and a narrower nasal aperture. Molara 2 presents a much higher face than Oriente B and both are closer to each other on neurocranial results. However, the five Uzzo fossils are more distinct to each other when only the neurocranium is considered. Uzzo 1 and Uzzo 5 totally overlap and have like Uzzo 2

a wider cranial vault. Uzzo 2 also presents a longer and lower vault. Uzzo 6 and Uzzo 9 are closer to Oriente B and San Teodoro 1; overall, all the Sicilian specimens except Uzzo 2 have a higher cranial vault. In general, the variability among Uzzo specimens is similar to other Upper Paleolithic and Mesolithic sites, as shown by the distribution of the samples from Zvejnieki (Latvia), Wadi Halfa (Sudan) and Tam Hang (Laos).

Cranial variation and morphological affinities among European Upper Paleolithic and Mesolithic groups

Results obtained considering only the complete Upper Paleolithic and Mesolithic European crania (Fig. 3) disclose that not only all the Sicilian skulls (except San Teodoro 1), but also all the Italian ones tend to concentrate together with both the Oberkassel individuals, Cro-Magnon 2

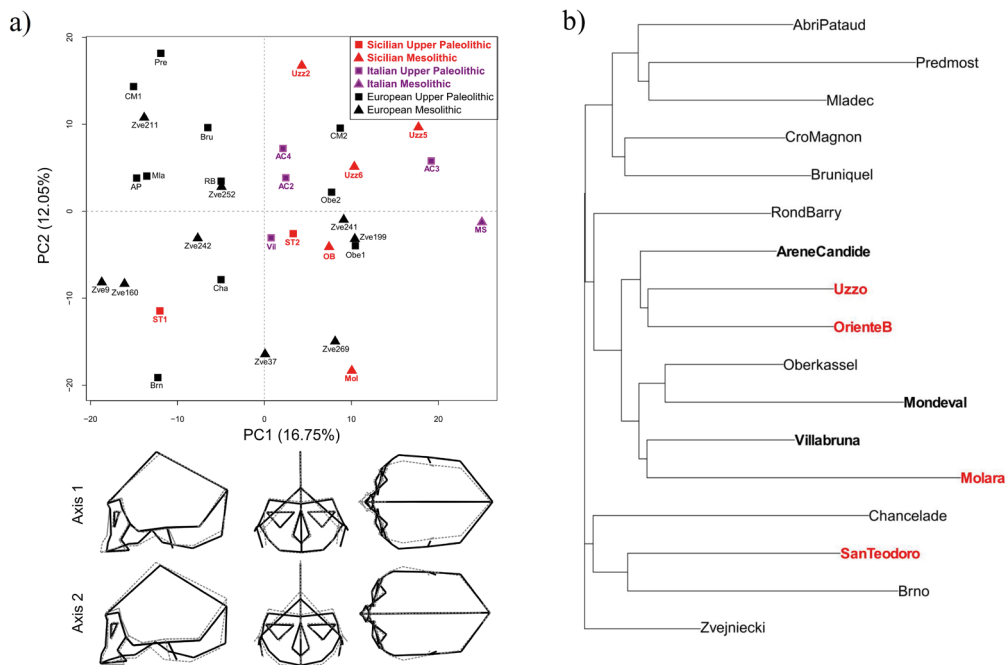


Fig. 3. Cranial variation among the subset of European Upper Paleolithic and Mesolithic groups, including the Sicilian samples: a) PCA based on Procrustes coordinates with shape changes. Landmark configurations (lateral, frontal and superior views) represent the highest (bold) and the lowest (grey) scores. Abbreviations are in Tab. 1. The specimens numbers are indicated only in the case of several specimens by site. b) Neighbor-Joining tree based on Procrustes distances (only the group centroids are represented to improve the readability). Italian specimens are in bold. The colour version of this figure is available at the JASs website.

and a few Zvejnieki specimens (Fig. 3a). Once again, San Teodoro specimens appear partially distinct from Sicilian Mesolithic specimens. Shape changes show again that San Teodoro specimens (especially ST1) have a more prognathic, taller and narrower face, a much narrower cranial vault and shorter mastoid processes. The Neighbor-Joining tree computed on Procrustes distances among specimens and groups (Fig. 3b) reiterates the same observation with San Teodoro and Mesolithic groups segregating within different clusters. San Teodoro shows its strongest affinities with Brno; Uzzo is tied to Oriente B and Molara to Villabruna, and they all together are relatively close to other Upper Paleolithic (Arene Candide) and Mesolithic (Mondeval de Sora) Italian specimens.

Cranial variation and morphological affinities among worldwide past and modern groups

Considering all samples (Fig. 4), the Sicilian material fits within the global variability of Old World past and extant specimens. San Teodoro specimens are strongly distinct from Mesolithic Sicilian sites and present much closer affinities with Upper Paleolithic specimens and Australo-Melanesian and African groups. They share a much narrower cranial vault, longer vault, more projected glabella, shorter and wider face, lower and wider orbits (Fig. 4a). Mesolithic Sicilian specimens are closer to other Mesolithic samples (Mondeval de Sora especially) and European and Asian samples. Uzzo and Mondeval de Sora have shorter and narrower face, wider and longer cranial vault.

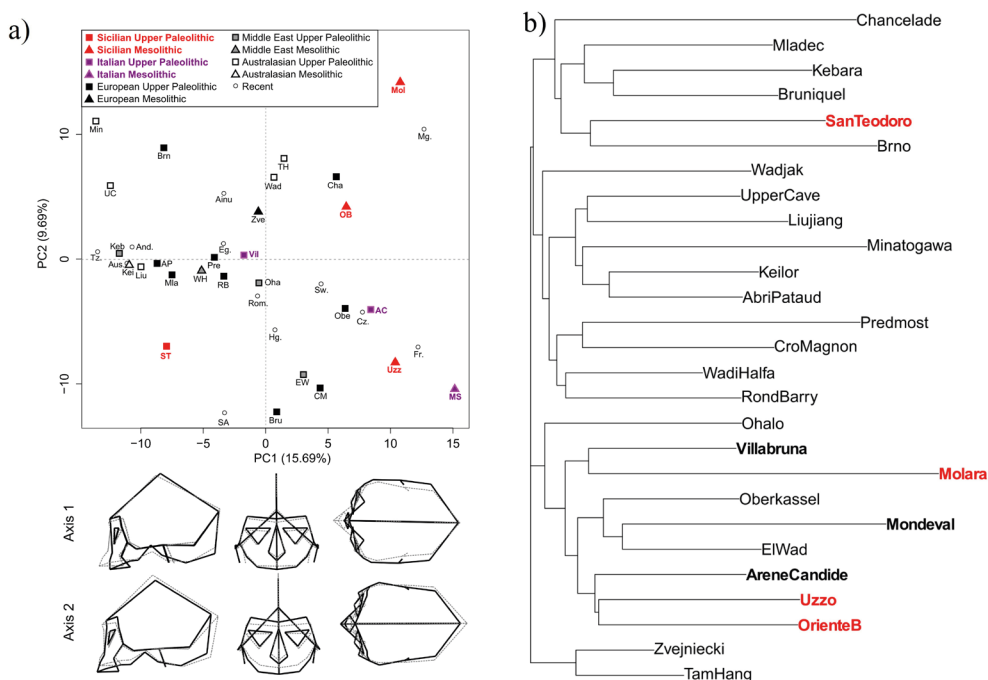


Fig. 4 - Cranial variation among all samples: a) PCA based on Procrustes coordinates with shape changes observed for the skull among all samples (only the group centroids are represented to improve the readability). Landmark configurations (lateral, frontal and superior views) represent the highest (bold) and the lowest (grey) scores. Abbreviations are in Tables 1 and 2. b) Neighbor-Joining tree based on Procrustes distances among cranial samples from Upper Paleolithic and Mesolithic (only the group centroids are represented to improve the readability). Italian specimens are in bold. The colour version of this figure is available at the JASs website.

A Neighbor-Joining tree computed on Procrustes distances among Upper Paleolithic and Mesolithic specimens and groups (Fig. 4b) underlines again the distinction between San Teodoro and Mesolithic specimens. San Teodoro presents affinities with Upper Paleolithic European specimens, especially Brno (Czech Republic). Oriente B and Uzzo are tied and relatively close to Molara and other Mesolithic specimens like Mondeval de Sora and Upper Paleolithic Italian (Villabrúna) and Israelian (El Wad and Ohalo) specimens.

Although some of our landmarks capture sexually dimorphic cranial areas (such as glabella or inion), morphological differences between males and females does not appear to have strongly influenced the pattern of morphological

differences observed between groups since no clear distinction was visually observable between males and females from all sites. Furthermore, male and female individuals from the same site are often very close to each other (see Supplementary Material Fig. S2).

Partial Mantel tests

A partial Mantel test calculated on Procrustes and geographical distance matrices (controlling for temporal distances) for a subset of 17 European Upper Paleolithic and Mesolithic groups only, produced a non statistically significant result, with $r = -0.1309$, and $p = 0.205$, excluding again that gene flow was the major mechanism influencing the variation among these groups.

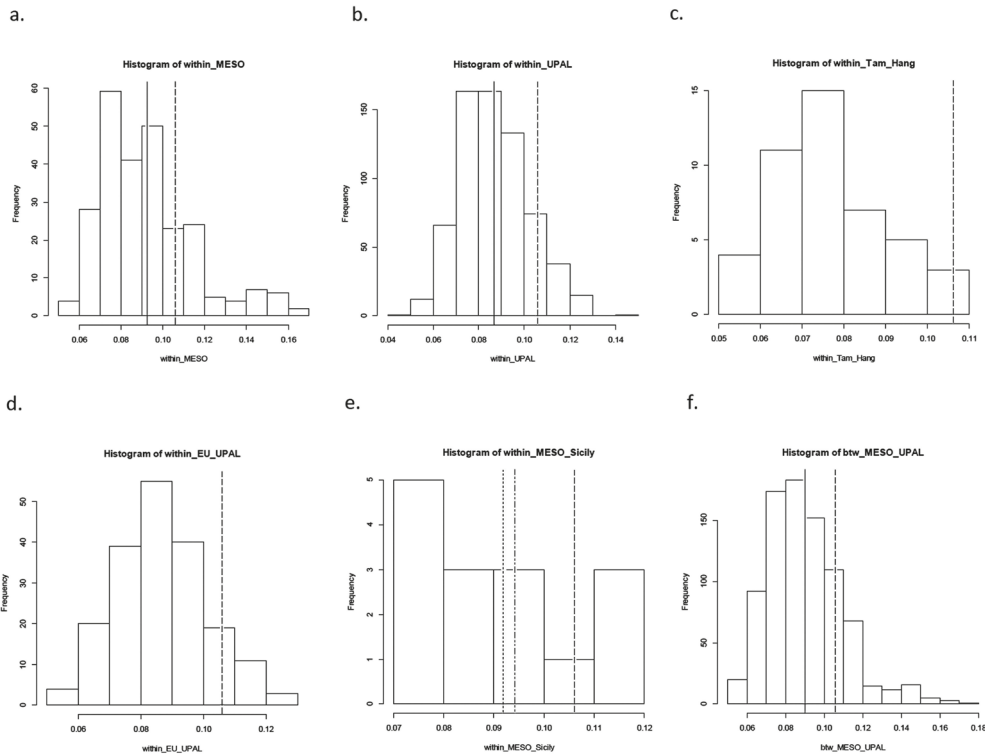


Fig. 5 - Pairwise Procrustes distances within and between samples. In a. and b. the dashed line represents the mean distance between San Teodoro (Upper Paleolithic) and Mesolithic Sicilian specimens, the solid line the mean within-distance of the group considered (all regions). In c. and d. the dashed line represents again the mean distance between San Teodoro and Mesolithic Sicilian specimens. In e. the dotted line represents the mean within-distance of the Sicily Mesolithic group, the dashed-dotted line the distance between San Teodoro 1 and San Teodoro 2 specimens, the dashed line the mean distance between San Teodoro and Mesolithic Sicilian specimens. Finally in f. the solid line represents the mean distance between Mesolithic and Upper Paleolithic (all regions), the dashed line the mean distance between San Teodoro and Mesolithic Sicilian specimens. The probabilities to find a Procrustes distance higher than the distance between Sicilian Upper Paleolithic and Mesolithic are: within Mesolithic: 0.22; within Sicilian Mesolithic: 0.27; within Upper Paleolithic: 0.12; within European Upper Paleolithic: 0.1; within Tam Hang: 0.02. The colour version of this figure is available at the JASs website.

A partial Mantel test calculated on Procrustes and temporal distance matrices (controlling for geographical distances) for the subset of 17 European Upper Paleolithic and Mesolithic groups only, produced a quasi-statistically significant result, with $r = 0.234$, and $p = 0.065$, suggesting the occurrence of some morphological time-related differentiation (e.g. across LGM transition).

A partial Mantel test on Procrustes and geographical distance matrices (controlling for temporal distances) for all the 27 groups, resulted in a correlation coefficient $r = -0.055$, with $p = 0.380$, indicating that gene flow was not the main factor producing the pattern of morphological similarity and that morphological variation among groups is not distributed according to a simple model of isolation-by-geographic distance.

Tab. 3 - Pairwise distances within and between samples.

Distance between ST1 and ST2:	0.094
Mean distance between ST1 and Sicily Mesolithic:	0.11
Mean distance between ST2 and Sicily Mesolithic:	0.1
Mean distance between Sicily Upper Paleolithic and Sicily Mesolithic	0.106
Mean distance between Upper Paleolithic and Mesolithic (all regions)	0.09
Mean distance within Mesolithic (all regions):	0.09
Mean distance within Upper Paleolithic (all regions):	0.087

A partial Mantel test on Procrustes and temporal distance matrices (controlling for geographical distances) for all the 27 groups, resulted in a correlation coefficient $r = 0.085$, with $p = 0.275$, indicating that time had not a major impact in producing the observed pattern of morphological relationships and that morphological variation among groups is not distributed according to a simple model of diachronic change.

Distribution of pairwise distances within and between Upper Paleolithic and Mesolithic samples

The distance between Sicilian Upper Paleolithic and Mesolithic is somewhat higher than the average within Mesolithic and within Upper Paleolithic distance (Fig. 5, Tab. 3). In other words, the chance of finding two specimens within any of these samples with a pairwise distance as high or higher than the distance that separates San Teodoro from the Sicilian Mesolithic is quite low and does support the idea of a major change between the two periods in Sicily. Accepting 0.05 as cut-off for an unlikely value, the distance between San Teodoro (Sicilian Upper Paleolithic) and Sicilian Mesolithic is within the range of observed within-group distances, with the exception of Tam Hang, so San Teodoro being part of that distribution cannot be excluded.

When compared to more homogenous subsamples (Tam Hang and European Upper Paleolithic), the distance between Sicilian Upper Paleolithic and Mesolithic is on the high side of the distribution. Thus, the chance of finding an equal or higher distance in Tam Hang is 2%,

while in the European Upper Paleolithic it is 10.5%. When compared to the pairwise distances between Upper Paleolithic and Mesolithic, the Sicilian Upper Paleolithic-Mesolithic distance is higher, meaning that on a worldwide scale it is less likely to find a pairwise distance as high as or higher than the one between the Sicilian Upper Paleolithic and the Sicilian Mesolithic. When compared to the European Upper Paleolithic, San Teodoro's average distance is lower than it is to the Sicilian Mesolithic. However, within the Sicilian Mesolithic 27% of pairwise distances are as high or higher than the one between San Teodoro and the Sicilian Mesolithic, which confirms a certain heterogeneity within the Sicilian Mesolithic.

All tests show then that the distance between the two San Teodoro specimens on the one hand, and the Sicilian Mesolithic specimens on the other, exceeds other distances, most importantly the distance between Upper Paleolithic and Mesolithic specimens within Europe and across all regions. However, they also show that the distance separating the two San Teodoro specimens from each other is quite high, higher than the average within – Upper Paleolithic distance across all regions, suggesting perhaps that this population was highly diversified to begin with. Overall however, the probabilities to find equal or higher distances within and between other subsamples, with the exception of Tam Hang, do not meet the minimum statistical threshold of 5%. Based on the relative difference in probabilities, these results hint at population change in Sicily, but do not strongly support it, statistically.

Discussion

The attention to the first *Homo* migrations in the ancient world has become a leit-motif of anthropological and archaeological research, favored also by recent developments in morphological and biomolecular analytical methodologies. The timing and paths of ancient human movements are now better understood, often reserving many surprises and the overcoming of preconceived ideas about the limited effectiveness of the first people in pursuing their objectives during their expansion movements. Furthermore, the peopling of an island - with the problems inherent to the crossing of the sea or of stretches not entirely practicable on the ground, as well as the population dynamics over time of the insularized and isolated population - is currently of great interest, and more and more data, sometimes controversial, is being collected.

To the present state of our knowledge, the hypothesis of a genetic discontinuity in Sicily across the Upper Paleolithic-Mesolithic transition does not currently seem to be well supported by other independent lines of evidence. In fact, much indirect evidence seem to support the opposite hypothesis, one of genetic continuity throughout the Upper Paleolithic-Mesolithic transition.

First, according to paleo-biogeographical reconstruction, significant episodes of sea level drop during the LGM between about 25,000 and 17,000 cal. years BP, with sea level being between 126 and 107m below the present level (Antonioli *et al.*, 2014), connected Sicily to the Italian peninsula by exposure of a today submerged sill in the Strait of Messina. These phenomena favored the dispersion of faunal elements from southern Italy, allowing the mammalian assemblage of the island to undergo a large turnover as well as a complete rearrangement (Masini *et al.*, 2008). The first people who travelled to Sicily took advantage of these episodes and presumably moved along the Tyrrhenian coastal sites in an ecologically dynamic phase during the late Upper Paleolithic period, and might have faced rapid and drastic ecological changes. All

the available dates of the earliest archeological sites are in accordance with the paleontological evidence of the arrival from continental Italy of the Castello Faunal Complex, with the oldest date of 23,000–20,500 cal. years BP based on a ^{14}C date for a specimen of *Equus hydruntinus* from Grotta di San Teodoro (Antonioli *et al.*, 2014). This suggests that human migration into Sicily could have occurred during the LGM, more precisely in the time span between 25,000 and 17,000 cal. years BP when the continuous presence of a land connection is supported by the most updated geological data accounting for isostatic and tectonic movements and erosion rate of the seafloor (Antonioli *et al.*, 2014). After 17,000 cal. years BP, the land connection through what is now known as the Strait of Messina (currently occupying a minimum depth of 81m) was interrupted by sea levels rising. Nevertheless, an overland passage of the Strait of Messina, as the one that presumably occurred during the LGM, might not represent a necessary condition for humans to reach Sicily: in fact, it is well known that humans were potentially able to cross substantial stretches of open sea (at least 90 km wide) at least since the time when they colonized Australia, roughly 65,000 years ago (Mellars, 2006; Clarkson *et al.*, 2017). However, as Antonioli *et al.* (2014, p. 111) pointed out, even “today the sea crossing to Sicily, although it is less than 4 km at the narrowest point, faces hazardous sea conditions, made famous by the Homeric myth of Scylla and Charybdis”.

Second, according to archaeological evidence, the Mesolithic of Sicily seems to be tightly linked to the Late Epigravettian at least in some typological facies (e.g., the Mesolithic of Epigravettian tradition). Furthermore, the combination of Late Epigravettian tradition with external cultural influxes produced new techno-typological tendencies both in Southern Italy and in Sicily at the onset of the Mesolithic. Northern Sauveterrian influxes combined with the Late Epigravettian “armatures-prevalent phylum” tradition produced a local Sauveterrian facies (microlithism, “Sauveterre-like” bilateral backed armatures) (Lo Vetro & Martini, 2012).

Microlithic convex backed tools and microlithic/ipermicrolithic geometries are referred only in Sicily to a further Mesolithic phylum related to the local Late Epigravettian tradition (Lo Vetro & Martini, 2012).

Also, funerary practices and subsistence patterns seem to confirm the Late Epigravettian-Mesolithic link: Mesolithic burials show many features in common with the late Epigravettian ones; they are single primary depositions, interred in shallow graves in a variety of positions, and contained few or no grave goods, with the presence of worked shells in some cases (e.g. at Grotta d'Oriente), thus suggesting a variability in funerary customs that could have resulted from the development of intra-cultural diversity between different Mesolithic groups (Mannino *et al.*, 2012). Mannino & Thomas (2009; quoted by Mannino *et al.*, 2012, p. 9) suggested that “archaeological evidence of changes in aspects of hunter-gatherer life ways as art and subsistence strategies supports the notion that new territorial divisions had developed in western Sicily by the late Mesolithic, culminating in the establishment of well-defined territories”. Mannino *et al.* (2012, p. 10) quoted also the study of Gazzoni & Fontana (2011) on burial practices in the Italian Peninsula and Sicily from the middle Upper Paleolithic to the Mesolithic, pointing out that “the most significant changes in funerary customs took place in the Late Glacial and early Holocene, probably as a result of social and territorial rearrangements, which might ultimately have been caused by environmentally-driven changes in subsistence strategies”. Concerning diet and subsistence, study of faunal assemblages and isotope analyses for late Upper Paleolithic and Mesolithic sites of Sicily showed that hunter-gatherers living in the island during the final stages of the Late Pleistocene and the Early Holocene consumed almost exclusively protein from terrestrial mammals, such as red deer, European ass and aurochs; only a slight increase in marine food exploitation (mainly coastal resources such as terrestrial and marine molluscs) occurred after the transition to the postglacial, with fishing and wildfowling constituting secondary activities

until the late Mesolithic, when the exploitation of marine resources increased and possibly even included the meat of stranded cetaceans (Cassoli & Tagliacozzo, 1982, 1993; Martini *et al.*, 2007; Mannino & Thomas, 2009; Mannino *et al.*, 2011, 2012, 2015).

Brewster *et al.* (2014, p. 7), in their cranio-metric analysis of the largest European Upper Paleolithic and Mesolithic samples studied to date, found a clear morphological discontinuity only between pre-Last Glacial Maximum and later (Late Glacial, Early and Middle Holocene) groups, concluding that “there is morphological continuity between late glacial and Holocene populations, a view supported by the archaeological record, which shows that many aspects of the Mesolithic extend back to the LGM (Bailey & Spikins, 2008). The archaeological boundary reflects a cultural response to post-glacial conditions. The Mesolithic has been, and will likely remain, a difficult period to define. Attempts to find distinctively Mesolithic features have repeatedly failed (Price, 1987). While microliths are ubiquitous during the Mesolithic, they are nonetheless present (albeit in smaller frequencies) during the Upper Paleolithic (Straus, 2002)”. Brewster *et al.* (2014, p. 8) wrote to concur with Price’s (1987) view that the “Mesolithic means simply early postglacial hunter-gatherers, nothing more”, but they pointed out also that “certain regions saw more intensive settlements at this time, as overall population size increased (Bocquet-Appel *et al.*, 2005)”. In fact, bioarchaeological evidence from several European sites reveal a possibly significant increase in population density for the entire Mesolithic period: estimates in the order of 0.02–0.07 people per km² were proposed for late Mesolithic populations (Clark, 1977, quoted in Cavalli-Sforza *et al.*, 1994), whereas estimates in the order of 0.00168 (Aurignacian), 0.00183 (Gravettian), 0.00257 (Last Glacial Maximum) and 0.00722 (Late Glacial) people per km² were proposed for Upper Paleolithic populations (Bocquet-Appel & Demars, 2000; Bocquet-Appel *et al.*, 2005), although these average figures could be severely biased and challenged by the visibility of the

sites, the recovery techniques, and errors in estimating the number of humans at a given time (Bar-Yosef, 2001).

The only line of indirect and independent evidence that could provide support for the hypothesis of a genetic discontinuity during the transition between Late Epigravettian/Late Glacial and Mesolithic/Early Holocene periods, might be represented by paleogenomic studies. In the last few years, developments in massive sequencing techniques allow the generation of an unprecedented amount of genomic data from past populations (e.g. Posth *et al.*, 2016; Mathieson *et al.*, 2018). Up to now, only two Palaeo-Mesolithic Sicilian specimens have produced published data: a first palaeogenetic study on Oriente B individual (Mesolithic, directly dated by AMS ^{14}C to 10,683–10,544 cal. years BP), restricted to mtDNA HVR1 region only, suggested that humans living in Sicily during the early Holocene could have originated from groups that migrated from the Italian Peninsula around the Last Glacial Maximum (Mannino *et al.*, 2012). Catalano *et al.* (2019) generated a whole genome ancient DNA data from the Oriente C individual (putative stratigraphic date of 14,210–13,770 cal. years BP). Results showed that Oriente C belongs to haplogroup U2'3'4'7,8,9. Genome-wide data show for Oriente C a strong genetic relationship with Western European Palaeo-Mesolithic hunter-gatherers (Catalano *et al.*, 2019), suggesting that the “western hunter-gatherers” was a genetically homogeneous population widely distributed from the Atlantic seaboard of Europe in the West, to Sicily in the South, to the Balkan Peninsula in the Southeast (Mathieson *et al.*, 2018). In the light of these findings, Catalano *et al.* (2019) pointed out that the Oriente B individual needs to be processed by a genome-wide approach looking for continuity or discontinuity with the Oriente C. At present, our morphometric results seem to depict a discontinuity scenario. This research focuses on the geometric morphometrics of Sicilian Upper Paleolithic and Mesolithic skulls in comparison to a wide sample of contemporary European and worldwide hunter-gatherers. Even if this

approach is suitable and reliable, a strong limitation of analyzing such ancient archeological horizons could be represented by the small size of the available sample.

Unfortunately, reliable genome-wide data from older Late Epigravettian (e.g. San Teodoro, directly dated by AMS ^{14}C to 15,232–14,126 cal. years BP) and Mesolithic individuals from Sicily are presently unavailable; such data might allow for a comparison with the results of Posth *et al.* (2016), who analyzed 55 complete human mitochondrial genomes of hunter-gatherers spanning about 35,000 years of European prehistory, finding not only an LGM genetic bottleneck, but also a substantial population turnover in Europe in coincidence with the climatic instability around 14,500 year ago. Reliable paleogenomic data for San Teodoro, dated as slightly older than the time of turnover of Posth *et al.* (2016), and for Mesolithic individuals from Sicily, if available, could demonstrate that this island also experienced a major population shift. Unfortunately repeated recent attempts of obtaining aDNA from San Teodoro specimens failed due to the absence of collagen tissue.

Conclusions

The results reported here underline a certain variability among the Sicilian Mesolithic specimens, as well as an evident distance from the presumed founders represented by Upper Paleolithic settlers (San Teodoro specimens) that have closer morphological affinities with other European contemporaneous individuals. It is important to point out that this study is based on a small sample size. It is hoped that a larger set of individuals will be available in the near future, allowing to test the hypothesis of population replacement between Upper Paleolithic and Mesolithic, and to provide further insight about the biological history of prehistoric Sicily. Nevertheless, results indicate that the morphometric approach is extremely precise for the definition of cranial diachronic variability; this methodological approach allows for a conservative study and the reconstruction of

convincing phylogenetic scenarios that will find more and more chances to be debated, with the same degree of effectiveness, and by determining the same interest, inside the scenarios obtained by ancient genomic sequences after DNA extraction from the most significant fossils.

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